

# Natura Fecit Saltum: Punctationalism Pervades the Natural Sciences



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**Abstract** Despite parallel revolutions of uniformitarianism in geology and gradualism in biology c200 years ago, it is now clear that rare events of large effect prevail in the natural world. While astronomical and geological phenomena are more overt (e.g. asteroid impact, supervolcanoes, earthquakes, tsunamis), the general and widespread prevalence of major genetic, ecological and climatic events, and their long-term effects on life on Earth is becoming more widely appreciated. Biogeography abounds with examples of rare dispersal events shaping the biota of volcanic islands; ecological studies are showing us how adaptation can happen rapidly in association with habitat change; genomic studies show that major adaptations and speciation can happen rapidly through selection on just a few genetic variants; ecology shows us how tipping points can lead to major and irreversible shifts in ecosystems; climate change is exacerbating the frequency and degree of extreme weather events all over the globe. An unfortunate corollary of climate change is that the long-term integrated effects of global warming are experienced most strongly in connection with the most extreme events.

## 1 Introduction—Huxley’s Dissent

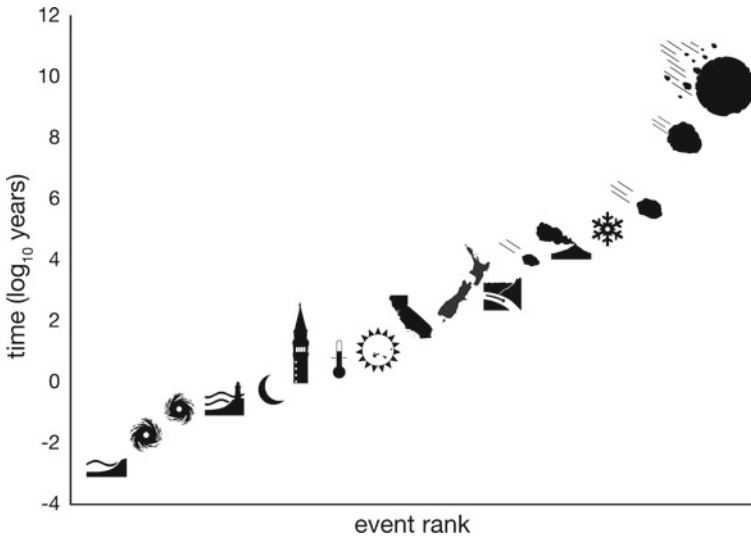
‘And Mr. Darwin’s position might, we think, have been even stronger than it is if he had not embarrassed himself with the aphorism, “*Natura non facit saltum*,” which turns up so often in his pages.’ Westminster Review, 1860 (Huxley 1906)

Change in nature, be it physical or biotic, is typically characterized as the result of continuous, gradual processes, immeasurable over our lifespan, accreted over eons of time. This concept was central to the thinking of Darwin (1859), building on the work of Hutton and Lyell (1830–1833). Their great insight was that large-scale past change could be explained in terms of small-scale ongoing processes (Penny and Phillips 2004), upending the orthodoxies of biblical creation in biology and

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**Fig. 1** Frequency of punctuational natural events: rank order plotted against  $\log_{10}t$ . From left to right: tides, Pacific cyclones, Atlantic hurricanes, king tides, lunar perigee, Acqua alta Venezia, El Niño, sunspots, San Andreas Fault, Alpine Fault, Cascadia Subduction Zone, 200 m asteroids, super-volcanoes, Milankovitch eccentricity cycle, 1-km asteroids, 10-km asteroids, Heavy Bombardment Era

catastrophism in geology [e.g. Cuvier and Whewell (Penny 2017), but see Gould (2002)]. Darwin portrayed the formation of adaptations and new species as the result of gradual change by natural selection; Hutton and Lyell saw mountain-building, erosion and formation of geological layers resulting from the imperceptibly slow processes of uplift, weathering and sedimentation. Thus, adaptation and speciation were effected by microevolution, and geological change by uniformitarianism, both over a timescale of millions of years.

Despite his own identification as ‘Darwin’s bulldog’, when first reading *The Origin of Species*, Thomas Huxley famously remarked: ‘you have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly’, and (with reference to organic chemistry as an example): ‘... I have a sort of notion that similar laws of definite combination rule over the modifications of organic bodies, and that in passing from species to species “*Natura fecit saltum*”.’ (Provine 1971).

The modern synthesis of evolution famously melded genetics (Dobzhansky 1937), systematics (Mayr 1942) and palaeontology (Simpson 1944). The first two of these evolutionists and their subsequent followers largely adhered to a more classical Darwinian gradualism, not attributing much evolutionary importance to macromutations (‘sports’), favoured by Goldschmidt (1940) as material to evolutionary change. Simpson was more pluralist, seeing a continuum of ground between gradualism and punctuationalism, perhaps reflecting his palaeontological background, which Gould was later to promote. Ongoing developments in these areas, as well as in climatol-

ogy, ecology and molecular genetics, increasingly suggest that natural processes are indeed, as Huxley perceived, actually rather ‘lumpy’, with the majority of change occurring during relatively brief, extreme events, punctuating periods of relative calm or stasis. Here, I review the widespread significance of these punctational events across all natural sciences (Fig. 1).

## 2 Extraterrestrial Events

Conceived after findings from the Apollo moon mission, and what would be the most cataclysmic event in Earth’s history if it were to happen again, is that of the Late Heavy Bombardment nearly 4 billion years ago (yBP). Although the narrowness of this event is now under question (Mann 2018), there was at least a period in early Earth history when our planet was pounded with asteroids, perhaps delaying, if not re-setting, the origin of life. Since then, at least some of the largest mass extinctions were probably the result of bolide impacts (Chapman and Morrison 1994). These include the famous Cretaceous–Paleogene (K–Pg) boundary dinosaur-extinction event 66 million years ago (Ma), linked to the Chicxulub crater and atmospheric soot (Bardeen et al. 2017). There is a strong inverse relationship between size of asteroid and impact rate; the biggest the events are the rarest, with 1-km asteroids hitting at  $c10^8$  year intervals. The Earth’s eccentric orbit, and obliquity and precession of its axis led to a period of Pleistocene glaciations, ongoing since 2.6 Ma. These have occurred on a cycle of  $\sim 10^5$  years over the last million years, and about  $2.5 \times$  that frequency before (Hodell 2016; Tzedakis et al. 2017), with both destructive and creative effects on the planet’s flora and fauna (Hewitt 2000, 2004; Jansson and Dynesius 2002; Wallis et al. 2016; Weir et al. 2016).

## 3 Geology

Geology provides many dramatic episodic events, epitomized by massive subduction zone earthquakes and ensuing tsunamis of the Pacific Rim. Tsunami have been shown to be responsible for deposition of deep sand beds in sea caves as well as further inland, making up the large part sedimentation in these places (Rubin et al. 2017). The huge tsunami generated by the 2011 East Japan earthquake transported a documented 289 species (16 phyla) of coastal species to the Hawaiian islands and western coast of North America, mostly by rafting (Carlton et al. 2017). The recent Kaikoura earthquake in New Zealand lifted the foreshore a few metres in places (Hamling et al. 2017), temporarily eradicating local intertidal and subtidal communities of kelp, molluscs and echinoderms. Major landslips, like the Usoy rock-slide of 1911, can create new lakes; Green Lake in Fiordland, New Zealand, was created 12,000–13,000 years ago when a 9-km block of mountains slipped down 700 m and

along 2.5 km (Graham 2008), and more recently the Dart River was dammed by an enormous rockfall, which locals felt as an earthquake.

Evidence strongly points towards volcanism (in Siberia in both cases) as the cause of two mass extinctions: the biggest of all at the Permian–Triassic (252 Ma) leading to global anoxia (Stordal et al. 2017), and the Triassic–Jurassic (201.5 Ma) (Percival et al. 2017). Fifteen planet-altering mega-eruptions have been identified over the globe, likely associated with extinctions of varying degrees (Witze 2017). Supervolcanoes such as Yellowstone, Toba and Taupo have the potential to be 3–4 orders of magnitude larger than the Mount St Helens eruption in 1980, with far-reaching effects on Earth's climate and biota (McDowall 1996). Super-eruptions (>1000 gigatonnes) have recently been estimated to occur as frequently as every 17 kyr on average (Rougier et al. 2018).

When the Straits of Gibraltar closed 6 Ma, the Mediterranean dried, leaving a basin 3–5 km deep in places, probably with a few hypersaline lakes and pans, until filling again some 700 kyr later (Hsü et al. 1977). Filling of the Black Sea through the Bosphorus probably occurred in a monumental flood some 7–8 kyr ago, turning a freshwater lake into marine habitat (Ryan et al. 1997). Erosion and tectonic uplift can lead to headwater capture (river piracy), transferring biota from one system to another, an important mode of range expansion and speciation in freshwater fishes (Craw et al. 2016; Tagliacollo et al. 2015; Waters et al. 2001).

In Derek Ager's words: 'the history of any one part of the earth, like the life of a soldier, consists of long periods of boredom and short periods of terror' (Ager 1973).

## 4 Biogeography

The colonization of new landmasses, particularly islands, is dominated by chance events, often happening soon after condition become habitable. Lack's 'first arrival' hypothesis is apparent from island radiations of groups that just happened to get there first and thus be able to adapt to multiple niches in the absence of other occupants (Lack 1947), and rapidly spread to nearby islands (Wilmshurst et al. 2011). Thus, finches radiated in the Galápagos (Schluter 2000) and became the honeycreepers of Hawaii (Freed et al. 1987), while ancestors of Californian tarweeds became the Hawaiian silverswords (Carlquist et al. 2003). Monophyletic radiations can dominate the fauna, such as *Anolis* lizards in the Caribbean, *Nesotes* beetles on the Canaries and picture-winged *Drosophila* on Hawaii (Emerson 2002). Lemurs and chameleons dominate the Madagascan fauna whereas New Zealand is known for radiations of ratites, reptiles, land-snails, earthworms, cicadas, moths, ensiferans, *Veronica*, *Ranunculus* and *Celmisia*, though depauperate in many other groups (Gibbs 2016; Wallis and Trewick 2009). New Zealand's freshwater fish fauna is dominated by galaxiids and gobiids (McDowall 2000), and Hawaii by gobiids (McDowall 2003), which happened to get there first, reflecting their diadromous life history (Burrige et al. 2012). Thus, island faunas can reflect a few unlikely chance events early

in their colonization. Once settled, plants and animals undergo rapid adaptive radiations, filling niches normally occupied by other groups on continents. Intriguingly, recent work on city park populations shows evidence of rapid morphological and genetical divergence in a lizard species, over the last century or more that cannot be attributed to drift alone (Littleford-Colquhoun et al. 2017).

## 5 Adaptation

Ironically, Darwin's own metaphor for natural selection-artificial selection by humans (Darwin 1859)—is evidence that morphological change can be effected rapidly in a wide range of species (DeLong et al. 2016; Ellner et al. 2011). Many classic natural examples of adaptation are also rapid and represent responses to human habitat modification (Alberti 2015; Bosse et al. 2017; Bradshaw and Holzapfel 2008; Carroll et al. 2007; Franks and Weis 2008; Palumbi 2001a, b; Rudman et al. 2017), including domestication (Zeng et al. 2017), physiological responses to pollution (van't Hof et al. 2016; Wright et al. 2013) and over-harvesting (Borrell 2013), resistance to drugs (Brown and Wright 2016), herbicides (Délye et al. 2013) and pesticides (Crossley et al. 2017), and introductions to new environments (Cattau et al. 2017; Gordon et al. 2015; Lee et al. 2011; Novy et al. 2013). These have sweeping local effects such that original populations can be completely replaced by genetically distinct ones in a few generations, or more widespread in the case of spread of viruses or plasmids carrying resistance factors. Recent work using *Tribolium* suggests that rapid evolution can be the cause of range expansion rather than merely a result (Szücs et al. 2017).

Change can be rapid when there is plentiful standing genetic variation for a quantitative trait, or 'soft sweep' (Crossley et al. 2017; Jain and Stephan 2017) and can be effected by change in gene expression as well (Becks et al. 2012; Huang et al. 2017; Passow et al. 2017; Rollins et al. 2015; Uusi-Heikkilä et al. 2017). Indeed, altering gene expression through quantitative trait selection can be a rapid mode of adaptive evolution, since the protein is already present (Goncalves et al. 2017; Margres et al. 2017; Mathieson et al. 2015; Nandamuri et al. 2017). Strictly speaking, the rapid sorting of existing polymorphism may not strictly constitute 'evolution' in its entirety, but it is certainly an important component and can happen on an ecological timescale (Lallensack 2018). A recent review detailed numerous examples of evolutionary changes associated with extreme climatic events (Grant et al. 2017).

Adaptation on islands can be particularly rapid due to intense selection caused by novel food, habitat and competitors. When the large ground finch, *Geospiza magnirostris*, established breeding on the small island of Daphne in the Galápagos, the resident medium-sized *G. fortis* underwent a sharp reduction in bill size over the course of two seasons, coinciding with a drought the previous year (Grant and Grant 2006). In contrast, termite-eating geckos on five islands created by flooding behind a dam showed parallel increase in head-size within 15 years, reflecting inclusion of larger prey items in the absence of competition following extinction of four larger

species (de Amorim et al. 2017). Another reptile showed a rapid change in perching behaviour when an invading congeneric competitor was introduced, resulting in a concomitant increase in toe-pad size as a result (Stuart et al. 2014). Rapid size increase on an even shorter timeframe has been documented in lake *Daphnia* in response to invasion by predatory zooplankton (Gillis and Walsh 2017).

Application of genomics is providing examples where rapid adaptation has been achieved through selection acting on a small number of genes (Lamichhaney et al. 2015, 2016; Rogers et al. 2017), in some cases caused by transposons (Brawand et al. 2014; van't Hof et al. 2016), or genes within inversions (see Speciation section). An example in steelhead trout (*Oncorhynchus mykiss*) shows rapid adaptation to land-locked lake conditions through change in transcription rates of four osmoregulatory genes within 14 generations (Aykanat et al. 2011). Such examples are particularly compelling when they can be shown to have happened repeatedly, in cases of convergent or parallel evolution (Arendt and Reznick 2008; Martin and Orgogozo 2013). In three-spine stickleback (*Gasterosteus aculeatus*), for example, repeated deletions in *Pitx1* have caused reduction in pelvic girdle structure associated with adaptation to freshwater habitat (Chan et al. 2010) by a single mutational leap. Different cave populations of tetras (*Astyanax*) show different 'regressive' loss of function mutations in the same pigmentation gene (*Mclr*) in separate cave systems, one of them, remarkably, homologous to the substitution leading to red hair in humans (Gross et al. 2009), as well as independent deletions in another gene (*Oca*) causing complete albinism (Protas et al. 2006). Populations of rock pocket mice (*Chaetodipus intermedius*) on dark substrates show different mutations at *Mclr* modulating adaptive melanism, while some populations utilise different loci altogether (Nachman et al. 2003). A recent case in *Anolis* lizards showed physiological, transcriptomic and genomic shifts after a single extreme winter (Campbell-Staton et al. 2017), recapitulating the classic work of Bumpus (1898). Repeated rapid evolution can happen on a seasonal basis (Becks et al. 2012) and has been shown for innate immune genes in *Drosophila* (Behrman et al. 2017).

As well as these examples of parallelism, a beneficial mutation in one species can be 'transported' to another through hybridization, as in the case of genes modulating bill size and shape in Darwin's finches (Lamichhaney et al. 2015, 2016), colour polymorphism in *Heliconius* butterflies (Dasmahapatra et al. 2012; Kronforst and Papa 2015), warfarin resistance in *Mus* (Song et al. 2011) and enhanced vectorial capacity in *Anopheles* mosquitoes (Fontaine et al. 2015). Repeated transport of low-armour *Ectodysplasin* (*Eda*) and low pigmentation (*Kitlg*) alleles, present at low frequency in the marine stock, has allowed rapid parallel evolution of the freshwater benthic form of *G. aculeatus* (Colosimo et al. 2005; Schluter and Conte 2009). There are even examples of horizontal gene transfer from bacteria and fungi into their phytophagous insect hosts (McKenna et al. 2016). Thus, a single mutational event can have far-reaching effects beyond the species in which it arose.

Major adaptations can often lead to incipient, or indeed, complete speciation (Wright et al. 2013). For example, movement of vertebrates onto land was preceded by a rapid threefold increase in eye size at 385–395 Ma, affording a million-fold increase in the volume of space in which objects could be seen (MacIver et al. 2017),

and launching several major new lineages. Developmental genetics has shown that major changes in body plan often derive from tinkering with cis-regulation of a small number of otherwise conserved gene families (Carroll 2008).

## 6 Speciation

Eldredge and Gould (1972) fervently championed (Gould 1980) the theory of ‘punctuated equilibrium’—the idea that phenotypic change tends to occur in bursts associated with cladogenesis, separated by long periods of stasis (Gould and Eldredge 1977). On a geological timescale, the punctuated evolutionary pattern is frequently upheld in morphologies preserved in fossils (Gould and Eldredge 1993; Jackson and Cheetham 1999; Stanley 1979; Vrba 1980). While some major geological boundaries (i.e. mass extinctions) are attributed to extraterrestrial and terrestrial geological causes (above), other links include marine transgression, atmospheric shifts, selenium depletion, and biotic changes, including the current human-induced event (Ceballos et al. 2017), subsequently promoting major new radiations (Lamsdell and Selden 2017), probably rapid ones (Ksepka et al. 2017), with new body plans exploiting new niches. The Cambrian explosion at 570 Ma led to a host of multicellular lineages in a very short space of time on a geological scale, most of which subsequently went extinct. These mass extinctions were followed by rapid phases of lineage diversification within certain groups (Simpson 1944), before slowing as the available niches became filled.

Punctuated equilibrium is undergoing something of a renaissance, given the recent availability of extensive molecular phylogenies and development of new analytical approaches (Hopkins and Lidgard 2012). A recent review (Pennell et al. 2014) distinguished two separate issues relating to evolutionary rate: (i) gradual versus pulsed evolution, and (ii) anagenetic versus cladogenetic evolution. Several examples supporting both concepts are presented (Uyeda et al. 2011), though that second is deemed hard to show on the basis of current data, particularly given the difficulty of morphologically cryptic species in fossils. This ‘quantum evolution’ of George Simpson has since been demonstrated in bird bill shape evolution (Cooney et al. 2017). Asteroid impact event at the K-Pg boundary led to sudden rapid diversification of bill shape (Simpsonian), followed by more gradual (Darwinian) evolution within lineages. Rapid radiations within three major superfamilies of frogs are similarly aligned with this event (Feng et al. 2017), though its implication in radiation of placental mammals is a matter of some debate (Liu et al. 2017; Penny and Phillips 2004). A recent analysis of the evolution of vertebrate body size used a maximum likelihood method to fit Lévy processes to comparative phylogenetic data and showed a pulsed mode of evolution with intervening stasis (Landis and Schraiber 2017). The oligochaete genus *Mesenchytraeus* appears to have undergone an explosive Pliocene radiation following uplift in the Pacific northwest, driven by habitat type (Lang et al. 2017). A pattern of rapid initial cladogenesis followed by slower lineage diversification could be a general observation in evolution of new groups (Rabosky and Lovette

2008), but may be caused by a correlation between the rate of phenotypic evolution and the rate of speciation, giving the impression that speciation is driving phenotypic divergence in a punctuated manner (Rabosky 2012). For example, ecological complexity and opportunity can drive rates of both phenotypic diversification and speciation. If these co-vary with each other across different lineages across a tree, it can lead to the perception that more change is associated with speciation.

Claims that Eldredge and Gould had uncovered a new evolutionary process were quickly repudiated: population genetics can easily explain geologically ‘rapid’ change over a few thousand generations (Charlesworth et al. 1982; Winsor et al. 2017; Wright 1931). Even Mayr’s seminal book made several mentions of ‘genetic revolutions’ (Mayr 1963). He took care, however, to clearly distinguish his view of post-founder effect genetic change, which results from re-organisation of variation already present, from Goldschmidt’s suggestion of systemic macromutations (Goldschmidt 1940).

Examples of comparatively rapid speciation in extant genera include dwarf planktivorous whitefish (*Coregonus*) repeatedly evolved from the normal benthic form (Dion-Côté et al. 2017), benthic and limnetic stickleback (*Gasterosteus*) from the anadromous form (Peichel and Marques 2017), and various divergent sympatric populations of trout (*Salmo*), charr (*Salvelinus*) and smelt (*Osmerus*), all formed in post-glacial lakes over the last several thousand years (Schluter 2000). The large species flocks of cichlid fishes in the African Rift Valley lakes show very little genetic divergence, implying rapid formation (Brawand et al. 2014; Meyer et al. 1990), despite an impressive array of feeding adaptations, patterns and colours. The 13 neotropical Midas cichlid species are only a few thousand years old, yet show attendant rapid evolution of opsins (Torres-Dowdall et al. 2017). One Nicaraguan crater-lake cichlid (*Amphilophus zalius*) probably arose from a more widespread species in the last 10,000 years (Barluenga et al. 2006). One of the fastest cases of speciation in vertebrates appears to have occurred in Baltic Sea flounder, where a demersal breeding form has evolved in low salinity conditions over the last 2,400 generations (Momigliano et al. 2017). A genetically homogeneous, selfing species of brooding sea star is hypothesized to have arisen in ecological time as a result of disruptive selection (Puritz et al. 2012). Phytophagous insects have the ability to switch host plants and speciate rapidly as a result (Coyne and Orr 2004). The tephritid fruit fly *Rhagoletis* switched from its native hawthorn (*Crataegus*) to apple (*Malus*) crops in the eastern USA in the 1850s, and has now switched back to novel endemic host hawthorn species with the introduction of infested apples into the Pacific northwest (Mattsson et al. 2015).

These examples of rapid divergence are often driven by adaptation to different ecological niches, but sexual selection is another likely driver, particularly in birds and fishes (Nosil 2012; Schluter 2000). More rapid still are potential examples of genetic isolation via *Wolbachia* infection in *Drosophila* and other insects (Charlat et al. 2003). Application of genomics to studies of speciation is also providing many examples of rapid speciation by ‘magic traits’, achieved either through pleiotropic effects of a few selected loci (Ferris et al. 2017), or hitchhiking of postzygotic isolation genes



with a strongly selected locus (Wright et al. 2013). Some studies find punctuation at the molecular level causing departures from a molecular clock (Pagel et al. 2006), echoing an early suggestion that the molecular clock may be episodic and driven at least partly by selection (Gillespie 1984). Ongoing *in vitro* studies using *E. coli* shows sustained molecular evolution, often with very rapid fixation of positively selected mutations, even in the face of environmental constancy (Good et al. 2017).

Gould was criticized for his dalliance with the extreme saltationist ‘chromosome repatterning’ ideas of Richard Goldschmidt (Goldschmidt 1940; Gould 2002), but there is good evidence that rapid speciation has happened: we should maintain a pluralist view on rates and mechanisms of speciation. Chromosomal rearrangements appear to play a big role, since they can have the effect of reducing recombination and maintaining linkage of desirable combinations of genes in the face of gene flow (Ortiz-Barrientos et al. 2016). Saltational speciation through structural rearrangements (Lewis 1966) and polyploidy are clear examples in plants (Soltis and Soltis 1999); as many as 80% of angiosperms may be polyploids (Soltis and Soltis 2012). More recently, inversions have been shown to play a role in rapid ecological speciation in animals too (Hoffman and Rieseberg 2008), including *Gasterosteus* (Jones et al. 2012), *Rhagoletis* (Powell et al. 2013) and butterflies (*Heliconius*, *Papilio*) (Joron et al. 2011). Although it has often been thought that polyploids might represent an evolutionary ‘dead end’, evidence is building that suggests that it can be of long-term significance (Van de Peer et al. 2017). Genomics has confirmed that tetraploidisation has happened at least four times in major chordate lineages: twice at the beginning of vertebrate evolution, again in the teleosts, and again in salmoniform fishes. Each of these fundamental events spanned a single generation, becoming fixed in the descendant lineages, giving these groups vast scope for innovation and evolution through redundancy in gene copy number (Ohno 1970).

Recent work is revealing the hybrid nature of many species (Mallet 2007), including our own, where there has been widespread introgression of genes from archaic hominids conferring physiological adaptations (Evans et al. 2006; Huerta-Sánchez et al. 2014). Merging of genomes can derive from a small number of matings, providing traits with far-reaching consequences, such as range expansion (Pfennig et al. 2016), or ‘transgressive segregation’ allowing exploitation of novel habitat (Rieseberg et al. 2003), both greatly reducing risk of extinction. Hybridization followed by recombination is an appealing and plausible way to explain the rapid emergence of new forms (Dittrich-Reed and Fitzpatrick 2013). Stabilization of hybridity can be rapid, leading to new species in a few tens of generations, in animals as well as plants (Grant and Grant 2014; Lamichhaney et al. 2018; Mallet 2007; Marques et al. 2017; Meier et al. 2017; Soltis and Soltis 1999; Stemshorn et al. 2011; Ungerer et al. 1998).

## 7 Ecology

Although ecological theory is largely concerned with gradual processes and theory based on equilibria, disturbance (e.g. fire, invasions, overgrazing, disease, drought, anthropogenic effects) (Darimont et al. 2015) has been crucial to shaping ecosystems and communities. These disturbances can compound to produce cataclysmic events, such as loss of forest to scrub or grassland, or over-running of coral reefs by algae, sponges or grazers (Scheffer et al. 2001). Temporal environmental variability reduces the value of predictions based on competition theory (Wiens 1977), just as genetic drift can scatter population gene frequencies away from expected equilibrium conditions. Ecological systems have limited resilience; perturbations can cause a threshold to be crossed, leading to a new ecological regime. Habitat modification and over-harvesting can lead to nonlinear population dynamics and feedback loops when systems are perturbed beyond a tipping point (Scheffer et al. 2012), beyond which they may never recover, as is often the case with overfishing (Hsieh et al. 2005; Travis et al. 2014). Over the last 15 years, southwestern Australia has seen a rapid loss of kelp forest as its coastal ecosystem has become ‘tropicalized’ by warming of the Indian Ocean (Wernberg et al. 2016). In combination, multiple stressors can have larger and less predictable effects. Overfishing of spiny lobster (*Jasus*) in Tasmania has allowed invasion of long-spined sea urchin (*Centrostephanus*) into the now warmer waters, whose overgrazing of kelp in turn threatens a catastrophic phase shift (Ling et al. 2009)

As in social and financial systems, ‘black swan’ events (unlikely events with profound consequences) happen more frequently than expected in natural systems: they are the ‘heavy tails’ of normal distributions of events (Anderson et al. 2017). They are usually (86% of the time) destructive rather than constructive, probably because there are fewer limits to the rate of population decline compared with growth. Disease has the potential for local extirpation, and pandemic epizootics can cause more widespread extinction. Nowhere is this more obvious than with anthropogenic introductions of pathogens into new areas, such as the effect of chytrid fungus on endemic amphibian populations (Stegen et al. 2017).

## 8 Climate

On a geological timescale, cyclical onset and ending of glaciation is very rapid, with each current glacial cycle representing some 0.002% of the Earth’s history. Yet on our own timeframe, such transitions would be imperceptibly slow: *Homo sapiens* has only been in existence through two such epochs. Some of the effects of post-glacial warming were, however, very immediate. Glacial lake outburst floods have devastating downstream effects, such as occurred in the Columbia River system at the end of the last glaciation, leaving signatures over a millennial timescale (Baynes et al. 2015; Larsen and Lamb 2016). The Straits of Dover were likely created by

draining of a lake from Doggerland at the end of the previous glaciation. Heinrich events, involving rapid glacial decay (counter-intuitively during cold periods), led to sudden discharge of huge quantities of ice from the Laurentide Ice Sheet into the North Atlantic. Recent modelling suggests that these events were triggered by very small climatic perturbations, with implications for our understanding of current melting of the Greenland and Antarctic ice sheets (Bassis et al. 2017), which also brings a threat of megadroughts to the Sahel region of Africa (Defrance et al. 2017). Current melting is itself exacerbated by the positive feedback effects of decreasing albedo-darkening of surface ice caused by residual particulate matter and growth of microbes and algae (Kintisch 2017). Receding glaciers can also cause abrupt re-routing of rivers, affecting landscape evolution (Shugar et al. 2017).

Our coastal cities and installations may not appear to be immediately threatened by a monthly sea-level rise of about 0.3 mm, with diurnal variation on a scale of several metres. Even monthly spring/king tides can differ by a metre from each other, swamping tiny annual increases. But hurricanes like Katrina, Sandy, Harvey and Irma are becoming more frequent, as are disastrous coincidences of tides, winds and low pressure (Garner et al. 2017), such as the North Sea Flood of 1953, which inundated low-lying parts of UK, Belgium and Netherlands. Current assessment practices tend not to take into account the multiplicative effects of coinciding high sea level and heavy precipitation (Moftakhari et al. 2017), the effects of which were only too evident in Harvey's impact on Houston.

A Sandy-like event had a return frequency of about 400 years in the year 2000, but that will fall to ~90 yrs by 2100 (Lin et al. 2016). Keeping time constant, a 100-year event will be 0.65–1.7 m higher in 2100 than in 2000, depending on the global climate change model used. This is already higher by about the same amount compared to AD 850. Thus, global warming may add a metre or more in sea level to an extreme event that cost \$50 billion the last time it occurred (Reed et al. 2015). Recent modelling shows a 1/500 yr event before 1800 to be a 1/5 yr event after 2030 (Garner et al. 2017). Ironically, the rarer and more extreme the event, the greater the added integrated effect of increased sea level. Likewise, modelling of precipitation accumulation (Neelin et al. 2017), convective available potential energy (Singh et al. 2018) and direct satellite observation (Taylor et al. 2017) show that extreme storm events get more frequent, and the biggest events get even bigger. El Niño events have caused repeated (1998, 2002, 2016) coral bleaching events on the Great Barrier Reef, with the most recent being the most extreme. As the frequency and intensity of these extreme events increases, the reef will likely reach a point beyond which recovery is not possible (Hughes et al. 2017).

As with our own mortality, demise usually follows a single major event (heart attack, stroke, disease) rather than old age alone. So it will be for coastal cities like New Orleans and Venice, and low-lying regions such as the Netherlands, Vietnam and Pacific island nations. Thinking about how we might mitigate future major events is of immediate importance to humanity. Although we must act to halt the slow, inexorable change caused by greenhouse gases, much of it will happen anyway because of inertia in the system.

## 9 Conclusion

Nature plays out as a series of major events, be it climatic or ecological, evolutionary or geological. We live in a jumpy natural world of serial catastrophism as opposed to true gradualism. The length and frequency of the events depends upon the process concerned; the common feature is that the duration is relatively very brief, and effects profound, compared to the long intervals of stasis or gradual change in between events. New adaptations can arise and become the new wild type over a few generations, yet remain in place for hundreds of thousands more; rapid speciation can happen on a scale of years or decades, though species typically exist for millions of years; dispersal events typically happen over periods of weeks or months, but resulting adaptive radiations may endure for millions of years; extreme weather events are measured by hours, but are separated by years or decades.

These extreme events are major purveyors of change through time. When we consider change through deep time, we are often looking at the results of numerous catastrophes or relatively sudden events telescoped together, rather than gradual change. This pattern extends to macroeconomic cycles of booms and crashes; even language (Atkinson et al. 2008) and cultural change (Kolodny et al. 2015) have been characterized as following a punctuated mode. There is a parallel here with Kuhn's portrayal of paradigm shifts in science (Kuhn 1996) and Marxist philosophy on the necessity for revolution to effect political transition. Although Darwin, Hutton and Lyell debunked biblical catastrophism, evidence for neocatastrophism on a shorter timeframe abounds. Although we live in a world of both gradual and punctuated processes, it is arguably the latter, as Huxley implied, that is responsible for most of the change in nature.

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